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Abstract

Evolutionary theory suggests two alternative ways in which competitive interactions could vary in response to different levels of food abundance. Competition theory suggests that aggression should be greater when resource availability is lower, as an evolutionary stable strategy to access food. Alternatively, energy allocated to aggressive interactions should increase when the available spectrum of food resources is wider, in turn allowing a greater selec- tion. We tested these hypotheses on a group-living herbivore, the Apennine chamois, *Rupicapra pyrenaica ornata*. We compared social, aggressive and vigilance behaviour and relevant endocrine correlates across three areas: two 'poorer' areas, i.e. with a lower availability of nutritious pasture, and a 'richer' one. In the richer area, we observed: (1) the largest group size/greatest proportion of young individuals in groups; (2) the lowest rate/intensity of aggression between individuals, at feeding; (3) the lowest duration of vigilance and proportion of 'costly' vigilance, i.e. postures performed without chewing food; and (4) the lowest levels of testosterone and cortisol metabolites, suggesting a lower endogenous aggressiveness/stress response. Our findings agree with the competition theory, suggesting a role of food depletion in increasing aggression between foraging individuals, as an evolutionary stable strategy, with cascading effects on group phenology, vigilance and stress.

ADDITIONAL KEYWORDS: aggression – Apennine chamois – feeding interference – group size – herbivores – intraspecific competition – *Rupicapra pyrenaica ornata* – social behaviour – stress – testosterone –vigilance.

INTRODUCTION

The availability of key resources is crucial for the sur- vival of wild species (Gause, 1932; Begon *et al.*, 2006). Food resources have influenced the evolution of physi- omorphological traits, e.g. digestive/feeding adapta- tions (Bowman, 1961; Lee, 1980; Tauber & Tauber, 1987; Hofmann, 1989; Meyer, 1989), and behaviour, e.g. social organization, mating system and spatiotem- poral behaviour (Jarman, 1974; Emlen & Oring, 1977; De Groot, 1980; Macdonald, 1983). In turn, variation in food availability is likely to influence key aspects of behavioural ecology of wild animals, with consequences at individual and population levels (e.g. Pettorelli *et al.*, 2002; Melis *et al.*, 2009; but see Forsyth, 2000). For example, populations with different levels of food abundance may show different rates of competition and stress but, to our knowledge, relevant information is not available for free-ranging animals.

Within a social group, individuals can compete for the access to crucial resources. A scramble com- petition occurs when food is consumed and depleted before being used by other individuals (e.g. Kiley- Worthington, 1978; Gillman & Crawley, 1990; Wise & Wagner, 1992). A contest competition (or feeding inter- ference) occurs through direct interactions between individuals (e.g. Walde & Davies, 1984; Symington, aggressive interactions between individuals can be considered as clues revealing intraspecific competi- tion (Miller, 1967). Evolutionary theory suggests two alternative ways through which competitive interac- tions could vary in response to different levels of food abundance. Classical competition theory suggests that intraspecific competition should be greater when availability of resources is lower (e.g. Volterra, 1926; Schoener, 1973; Titman, 1976). Accordingly, experimen- tal variations of food supply have provided evidence for intraspecific competition by resource exploitation when resources are scarce (Taitt & Krebs, 1981; Krebs *et al.*, 1986; Boyce, 1989). Yet, a

greater level of aggres- sive interactions between individuals can be expected (Sirot, 2000). Alternatively, the energy allocated in competitive interactions could increase along with the value of a disputed resource (Parker, 1974; Enquist *et al.*, 1985; Shopland, 1987). For example, according to Geist (1978), a great availability of resources can be expected to lead individuals to invest especially in body growth (e.g. weaponry), reproductive activities and social behaviours, whereas if resources are scarce, individuals should limit costly activities, e.g. social interactions. If so, agonistic interactions between indi- viduals would increase if resources were unlimited (Caraco, 1979; Goss-Custard *et al.*, 1984). Determining which hypothesis is supported by data would help us to understand how the variation in the abundance of food resources, e.g. triggered by environmental modifi- cations or climatic changes, might affect key aspects of social behaviour.

Variation in food abundance, e.g. food depletion, could elicit cascading effects on both physiology and social behaviour. For example, the group size of gre- garious foragers can be reduced if resources are scarce, thus limiting inter-individual feeding interference or scramble competition. Likewise, an increase of social stress may be expected, as a result of either a higher rate of aggression or a limited access to resources *per se* (Kelley, 1980). In turn, food depletion can have negative effects on both physiology and behaviour. Behavioural responses can lead individuals to divert their attention to a stressful factor, with the suppres- sion or reduction of other activities, such as feeding and reproduction (Reeder & Krämer, 2005). Although the main role of vigilance behaviour is considered to be an antipredator ploy (Beauchamp, 2015), it could also be an indicator of social stress, leading to trade- offs with foraging behaviour (Berger, 1978; Caraco, 1979; Underwood, 1982). Vigilance could lead to dif- ferent alertness postures by individuals, which imply different potential costs. Foraging individuals can perform either a 'routine vigilance' (i.e. an individual monitors the environment, e.g. Fortin *et al.*, 2004b) or an 'induced vigilance' (i.e. an individual adopts alert- ness postures after an outer stimulus, e.g. Blanchard & Fritz, 2007). Often, individuals keep on chewing while performing routine vigilance, whereas induced vigilance usually involves an interruption of chewing (Fortin *et al.*, 2004b; Blanchard & Fritz, 2007). In turn, vigilance postures without chewing are likely to limit the food intake more than those where chewing is not interrupted (Underwood, 1982; Blanchard & Fritz, 2007). If so, a greater feeding interference between conspecifics might lead to greater levels of vigilance, interfering with foraging and, in turn, determining additional energetic costs to individuals.

Aggressive behaviour is linked to the steroid hor- mone testosterone (Rohwer & Rohwer, 1978; Creel *et al.*, 1992; Pasch *et al.*, 2011; Martin *et al.*, 2013) which, in turn, can elicit immunosuppression (Folstad & Karter, 1992; Barnard *et al.*, 1996; Decristophoris *et al.*, 2007). Physiological responses to stress include an increase in the concentration of glucocorticoids or their metabolites (Möstl & Palme, 2002; Sheriff *et al.*, 2011). Secretion of glucocorticoids by the neuroendo- crine system can reflect the effects of several varia- bles, ranging from climate parameters (Bubenik *et al.*, 1983; Saltz & White, 1991; Konjević *et al.*, 2011) to behavioural traits (e.g. mating competition; Mooring *et al.*, 2006; Corlatti et al., 2012, 2014; Pavitt *et al.*, 2015, 2016). Long-term (chronic) production of high levels of glucocorticoids can also reduce survival and reproductive success, e.g. through the suppression of the immune function (Sapolsky, 1992; Möstl & Palme, 2002; but see Boonstra, 2013).

We evaluated the potential cascading effects of resource depletion on key aspects of social behaviour of a mountain-dwelling herbivore, the Apennine chamois, *Rupicapra pyrenaica ornata*. Recently, changes in the vegetation have been documented on the upper mead- ows of the central Apennines, with a local reduction of pasture quality for mammalian herbivores (Lovari *et al.*, 2014; Corazza *et al.*, 2016). Pasture depletion resulted in a high winter mortality of kids, for the 'vul- nerable' [*sensu* International Union for Conservation of Nature (IUCN); Herrero *et al.*, 2008] Apennine chamois, in the core of its historical distribution (Lovari *et al.*, 2014; Ferretti *et al.*, 2015; Scornavacca *et al.*, 2016). The negative effects of changes in weather phenology on vegetation grazed by chamois (Ferretti *et al.*, 2018), the spread of unpalatable tall grasses in secondary meadows (Lovari *et al.*, 2014; Corazza *et al.*, 2016) and increased resource exploitation by red deer, *Cervus elaphus* (Lovari *et al.*, 2014; Ferretti *et al.*, 2015), have been suggested as factors underlying pasture depletion, with subsequent negative effects on population dynamics.

We took advantage of a quasi-experimental situa- tion to test the effects of pasture depletion on levels of grouping behaviour, intraspecific aggression, vigilance and endocrine correlates, by comparing behavioural and physiological indices across areas with different levels of nutritional quality of pasture. We compared two 'poor' areas, i.e. with a lower availability of nutri- tious pasture, with a 'rich' area, i.e. with a greater

availability of nutritious vegetation (cf. Ferretti *et al.*, 2015; Scornavacca *et al.*, 2016). Evolutionary theory suggests alternative sets of predictions of the effects of different levels of resource availability/quality on social behaviour, aggression, vigilance and endogenous response to stress. We could expect that feeding interference would be greater in the poor sites than in the rich one, because individuals should increase direct competition for the limited food (hypothesis 1; Sirot, 2000). If so, in the rich area we would expect: the largest groups (prediction 1a); the lowest frequency and intensity of aggression between chamois (prediction 1b); the lowest frequency and duration of vigilance behaviour (prediction 1c); and the lowest levels of faecal cortisol and testosterone metabolites (prediction 1d). Conversely, we could expect higher feeding interference in the rich site than in the poor ones, because individuals should invest more energy in aggressive interactions where resources are not limited (hypoth- esis 2; e.g. Parker, 1974). If so, in the rich area there would be: smaller groups (prediction 2a); the highest frequency and intensity of aggression between chamois (prediction 2b); the highest frequency and duration of vigilance behaviour (prediction 2c); and the highest levels of faecal cortisol and testosterone metabolites (prediction 2d).

MATERIAL AND METHODS

Study areas and populations

Our study was conducted in three areas (area P1, upper Val di Rose, ~40 ha, 1700–1982 m asl, 41.75000°N, 13.91666°E; area P2, upper meadows of Mt. Amaro, ~20 ha, 1650–1882 m asl, 41.76666°N, 13.87500°E; and area R, upper meadows of Mt. Meta, ~30 ha, 2100– 2242 m asl, 41.69166°N, 13.92500°E; Fig. 1) within the core of the Abruzzo, Lazio and Molise National Park (ALMNP; central Apennines, Italy). The three sites lie in the same elevational belt (Primi *et al.*, 2016), in the temperate oceanic bioclimate, lower orotemper- ate thermotype and lower/upper humid ombrotype (Pesaresi *et al.*, 2014), and are all covered by grasslands dominated by forbs and/or graminoids. Nevertheless, the three sites have different extents of vegetation cover (Ferretti *et al.*, 2015). Area P1 includes palata- ble graminoids (35.5%, mainly *Festuca* spp.), unpalat- able graminoids (24.9%, *Brachypodium genuense*) and forb-dominated patches (15.2%, e.g. *Trifolium* spp., *Ranunculus apenninus*, *Plantago atrata*; Lovari *et al.*, 2014). Area P2 includes palatable graminoids (57.7%, mainly *Festuca* spp.), unpalatable graminoids (11.1%,
B. genuense) and forb-dominated patches (15.1%, e.g. *Anthyllis vulneraria*, *Medicago lupulina*, *Hippocrepis comosa*). Area R includes forb-dominated patches (24.5%, e.g. *Trifolium* spp., *A. vulneraria*), palatable graminoids (38.7%, mainly *Festuca* spp.) and unpalat- able graminoids (1.0%, *B. genuense*). Rocks/screes with sparse vegetation are also present in each site (area P1, ~25%; area P2, ~15%; area R, ~36%; Ferretti *et al.*, 2015).

High-quality, cold-adapted forb patches domi- nated by *Trifolium thalii* and other legumes are the most nutritious food resources for chamois (Ferrari *et al.*, 1988; Lovari *et al.*, 2014), as well as the most selected ones (Ferrari *et al.*, 1988; Ferretti *et al.*, 2014). Forb-dominated patches are more abundant in area R (24.5% of cover) than in areas P1 and P2 (~15% of cover), whereas patches dominated by unpal- atable *B. genuense* are widespread in areas P1 and P2 (~11–25%) but very rare in area R (~1%) (Ferretti *et al.*, 2015). In female chamois, the volume of forbs in the diet (P1, ~40%; P2, ~47%; R, ~60%; Ferretti *et al.*, 2015), the volume of nutritious plants in the diet (P1, ~5.5%; P2, ~6%; R, ~9%; Ferretti *et al.*, 2015) and feeding efficacy, i.e. number of bites per step per minute (P1, ~8; P2, ~12; R, ~14; Ferretti *et al.*, 2015), were the greatest in area R. In contrast, the volume of graminoids in the diet (P1, ~55%; P2, ~45%; R, ~35%; Ferretti *et al.*, 2015) was the lowest in area R, suggest- ing that female chamois were better fed in area R. In turn, frequency/intensity of suckling behaviour and survival of chamois kids were greater in area R than in areas P1 and P2 (Ferretti *et al.*, 2015; Scornavacca *et al.*, 2016).
A great density of wild ungulates, i.e. red deer (Ferretti *et al.*, 2015), wild boar, *Sus scrofa* (Fabbri *et al.*, 1983), and, to a much lesser extent, roe deer, *Capreolus capreolus* (Latini *et al.*, 2015), was present in the core area of the ALMNP. Although red deer were present at the same elevation as chamois in areas P1 and P2, they were not in area R, where they inhab- ited lower elevations than chamois (Lovari *et al.*, 2014; Ferretti *et al.*, 2015). Thus, grasslands of areas P1 and P2, but not those of area R, were grazed by red deer at high densities, with additional negative effects on vegetation cover and food availability for chamois (Ferretti *et al.*, 2015). In turn, the pasture quality and quantity differed greatly amongst sites, being richer in area R than in areas P1 and P2.

In the warm months, mixed groups of female Apennine chamois, yearlings and kids graze on alpine meadows, whereas males are solitary, living in forests at lower elevations (except during the rut in November and December, when they join the groups of females and juveniles) (Lovari & Cosentino, 1986). No chamois was artificially marked. A minimum of 32 (in 2014) and 21 (in 2015) chamois (i.e. the maximal number of indi- viduals observed at the same time) were present in groups with females, yearlings and kids in area P1; 35 (in 2014) and 29 (in 2015) individuals were present in area P2, and 69 (in 2014) and 78 (in 2015) individuals were present in area R. During the last decade, cham- ois numbers have decreased in areas P1 and P2 (> 50% decrease in area P1 and > 20% decrease in area P2; Ferretti *et al.*, 2015), because of heavy winter mortal- ity of kids, which was related to lower maternal care and, ultimately, to lower food availability for females (Lovari *et al.*, 2014; Ferretti *et al.*, 2015; Scornavacca *et al.*, 2016). Conversely, an increase in the population of chamois was recorded in area R, where only five or six males were present in 1975s–1980s, with no mixed group of females, yearlings and kids (S.L., personal observations).

Female ungulates are philopatric, and their emi- gration is an infrequent event (Bocci & Lovari, 2011; northern chamois *R. rupicapra*: Loison *et al.*, 1999, 2008). In turn, female chamois with morphologically distinct features (e.g. horn morphology, a broken horn, scars; Lovari & Rolando, 2004: 78) did not appear to move between our study sites. Moreover, preliminary data based on VHF/GPS radio-tracking support the local herd/site fidelity of female chamois (Latini *et al.*, 2013).

In ALMNP, potential predators of chamois are grey wolf, *Canis lupus*, Apennine brown bear, *Ursus arc- tos marsicanus*, and golden eagle, *Aquila chrysaetos*, although predation on chamois was negligible (< 2% for wolf, Grottoli, 2011; Patalano & Lovari, 1993; 0.05% for brown bear, Ciucci *et al.*, 2014; uncommon and restricted mainly to kids, for golden eagle, Scornavacca & Brunetti, 2015). It was assumed that predation pres- sure on chamois was comparably scarce across all three areas and that the three sites did not differ regarding accessibility to predators, which visited all our study areas (our observations; wolf, Mancinelli *et al.*, 2018; brown bear, Maiorano *et al.*, 2015; golden eagle, Artese *et al.*, 2017).

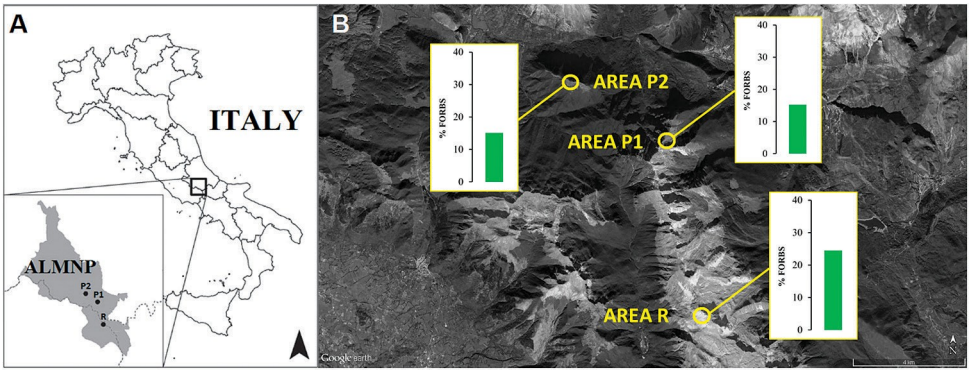


Figure 1. A, locations of study areas within the Abruzzo, Lazio and Molise National Park (ALMNP). B, relevant availability of nutritious pasture for chamois. Map data: Google, Digital Globe.

Behavioural data

Behavioural observations were conducted from July to October, in 2014 and 2015, from dawn to dusk. We performed 6–8 h of observations each day, for at least 7–8 days at each site during each month. We made an effort to balance sampling across sites, months and times of the day. Chamois were observed using binocu- lars (Nikon 10 × 30, Zeiss 15 × 70) or spotting scopes (Nikon 20–60×), at a distance of 50–200 m, depending on the terrain and range of vision. In our study area, chamois were habituated and could be approached up to 30 m (Bruno & Lovari, 1989; S. L., unpublished data) without showing alert behaviour (staring in the direc- tion of the observer or orientating their ears to him or her, and raising the tail as a sign of alarm; Lovari, 1985). However, we avoided recording data whenever we felt that the animals were reacting to our presence (cf. Winnie & Creel, 2007).

Our hypotheses have been focused on females, because: (1) pasture quality is particularly important to nursing females and weaning kids, which in turn are key drivers of population dynamics; and (2) except during the rut, most adult males are solitary, living on steep, forested slopes, thus escaping observational opportunities on a regular basis. Aggressive interac- tions among females (≥ 2 years old) were assessed through continuous focal group sampling (Altmann, 1974), by two or three observers, on foraging groups of females, yearlings and kids. Amongst group-living species, aggressive interactions should be relatively rare events within the overall time budget (e.g. birds: Caraco, 1979; mammals: Molvar & Bowyer, 1994). Dawkins (2007: 93) suggests longer sampling bouts to record infrequent events. Thus, we observed each focal group for ≥ 30 min, depending on group movements and visibility. Whenever possible, when the group did not split, we continued observing the focal group up to a maximum of ~6 h. Each focal group observation bout was divided into 5 min sampling periods, to record variation in group size and structure (number of adult and subadult females; number of yearlings; number of kids; number of adult and subadult males), which were assessed by instantaneous scan sampling (Altmann, 1974). We considered a group as at least 2 animals staying in sight and less than 40 m apart from each other at the time of observation (e.g. Krämer, 1969; Bruno & Lovari, 1989).

We recorded all the occurrences of aggressive interac- tions performed between grazing females during each 5 min sampling period using an mp3 dictaphone. For each aggression event, we recorded the date and time (in hours and minutes), age class of the opponents, type of interaction and behavioural patterns used by each individual. Four age classes were assessed according to Lovari (1985): subadult, i.e. 2–3 years old; 4–5 years old; 6–8 years old; and ≥ 9 years old. The type of inter- action was defined as a single aggression (a dominance pattern followed by an immediate submission/escape by the opponent) or a sequence (a series of consecutive dominance behaviour patterns performed by both oppo- nents). The latter case implied that the attacked indi- vidual reacted to the aggressor, thus we considered it as an escalation. Dominance and submissive behaviour patterns (Lovari, 1985) performed by female chamois were recorded. Dominance patterns include both indi- rect and direct forms of aggression to intimidate/dis- place rivals (Lovari, 1985). Indirect forms involve visual dominance postures (Lovari, 1985). Direct threats, such as approaches/chases, are the least ritualized and may include attempts at physical contact, although this is rare (Locati & Lovari, 1990). Submissive patterns include withdrawal and several ritualized, submissive postures, e.g. low stretch (Lovari, 1985). We excluded vocally based patterns because of the complexity in their detection and interpretation (Lovari, 1985). Dominance behaviour patterns of female chamois were divided into direct and indirect forms of aggres- sion (hereafter threats and displays, respectively; e.g. Walther, 1974; Schaller, 1977), to evaluate the inten- sity of interference. Threats were considered more intense, less ritualized forms of aggression than dis- plays (Walther, 1974; Schaller, 1977; Lovari *et al.*, 2015; in Apennine chamois: Lovari, 1985).

Vigilance behaviour was assessed by continuous focal animal sampling (Altmann, 1974), by two or three observers, on foraging females. Given that vigi- lance events are more frequent than agonistic events (e.g. birds: Caraco, 1979; mammals: Molvar & Bowyer, 1994), we used shorter sampling periods to record them (Dawkins, 2007: 93). Observations were con- ducted in 10 min bouts (e.g. Favreau *et al.*, 2018). Each bout was divided into 1 minute sampling periods, to record position and variation of group size and struc- ture. Group size and structure (number of adult and subadult females; number of yearlings; number of kids; number of adult and subadult males) and the distance to the nearest cliff (i.e. distance from escape terrain: 0–25, 25–75 or > 75 m) were assessed by instantaneous scan sampling (Altmann, 1974). We recorded the num- ber of head lifts performed by a female chamois during each 1 min sampling interval. The age class of the focal female was assessed as above. We considered a head lift when a female interrupted grazing and raised her head above her shoulders while scanning (e.g. Lipetz & Bekoff, 1982; Bruno & Lovari, 1989). For each head lift, we recorded date, time (hours and minutes), dur- ation (in seconds) and type: chewing (the individual keeps on chewing while scanning), no chewing (the individual does not chew while scanning) or indeter- minate (we could not see the mouth of the individual). Chewing was considered a clue to evaluate the cost of vigilance; head lifts where individuals do not chew are expected to interfere with foraging processes more than those where chewing continues (see Introduction; Underwood, 1982; Fortin *et al.*, 2004a). We avoided recording vigilance behaviour of the same individual on the same day; we observed chamois that could be distinguished by their respective positions on the slope (Frid, 1997), while another observer monitored those that had already been sampled. Small morphological differences (horn patterns, e.g. broken horns; coat/colour features, e.g. scars/spots; Lovari & Rolando 2004: 78) also helped to reduce the probability of recording data from the

same individual repeatedly on the same day (Lovari *et al.*, 2014; Ferretti *et al.*, 2014; 2015).

Endocrine data

The assessment of faecal hormone metabolites is a non- invasive tool, which provides unbiased results because the animal is not stressed by handling (Millspaugh & Washburn, 2004; Sheriff *et al.*, 2011). In addition, it can provide reliable information on basal endocrine levels of wild species, representative of long-term lev- els (Millspaugh & Washburn, 2004; Sheriff *et al.*, 2010). Faecal samples of female (2 years old) and year- ling chamois were collected from July to October 2015, to assess contents of faecal androgen metabolites and faecal cortisol metabolites as hormonal indicators of aggressiveness and stress, respectively (cf. south- ern chamois: Dalmau *et al.*, 2007; northern chamois: Corlatti et al., 2012, 2014; Zwijacz-Kozica *et al.*, 2013; Hadinger *et al.*, 2015). We observed grazing chamois and collected fresh faeces immediately after we saw a defecation event, at a distance of up to ~50 m. We put each sample into a plastic bag and stored it in a portable freezer box, which prevented changes of steroids attributable to the air temperature and immunoreaction of metabolites (Möstl *et al.*, 1999). The date, time (in hours and minutes) and age class (yearling, subadult female or adult female) of the chamois were recorded. Faecal samples were frozen at
−20 °C immediately after returning the field, no later than 10 h from collection (Ezenwa *et al.*, 2012; Corlatti *et al.*, 2012, 2014). We tried to balance faecal sample collection by the month, time of day and chamois age class. We avoided the repeated collection of samples from the same individual on the same day.
Extraction and determination of faecal steroids were conducted as reported by Pecorella *et al.* (2016) for fallow deer, *Dama dama* (see *Determination of fecal steroids*; Supporting Information).

Statistical analyses

Focal group bouts that lasted < 15 min and focal ani- mal bouts that lasted < 5 min were discarded from the analyses. Short bouts occurred when the focal group or individual moved away from our sight, or when poor weather (e.g. fog) limited our range of vision. Overall, we analysed 202 focal group bouts to assess grouping pat- terns and female–female aggression (~543 h of observa- tion; mean ± SE: 2.7 ± 0.1 h per group), 851 focal animal bouts to assess female vigilance (~120 h of observation; mean ± SE: 8.5 ± 0.1 min per individual) and 116 faecal samples (area P1, *N* = 5; area P2, *N* = 15; area R, *N* = 96 samples) of female and yearling chamois to assess endo- crine correlates. Collection of faecal samples in poor areas was limited by the low population size of chamois. Owing to the the small sample sizes at sites P1 and P2,
i.e. sites with lower pasture quality, we pooled them for comparisons with area R, i.e. the site with greater pas- ture quality, to assess endocrine differences.

We investigated differences in patterns of chamois social behaviour (grouping, aggression and vigilance) and hormone levels across study areas through gen- eralized linear models and generalized linear mixed models (GLMs and GLMMs, respectively; Zuur *et al.*, 2009). Statistical analyses were conducted using the information-theoretic approach (Burnham & Anderson, 2002), by evaluating multiple competing a priori hypotheses, for each indicator. In addition to food availability, previous studies also identified influ- encing factors of grouping, aggression, vigilance and hormone levels (Supporting Information, Table S1). We could not discard, in advance, any combination of these variables, because all the relevant hypotheses could be meaningful biologically. Thus, we first performed a model selection (see *Model selection*; Supporting Information), for each indicator, to rank all possible models, because each of them could represent a dif- ferent plausible a priori hypothesis. We modelled ten different response variables separately (Supporting Information Table S2). Error distributions and link functions used to model each response variable are listed in the Supporting Information (Table S2).
For each indicator, the global model included all the biologically meaningful fixed effects (Supporting Information Tables S1 and S2). We considered the site as a predictor to evaluate the role of pasture availability (reference category: area P2, for behavioural data; areas P1 + P2, for endocrine data). In addition, we included a set of different controlling predictors, depending on the indicator (see *Fixed effects in global models*; Supporting Information). Although we minimized pseudoreplica- tion of collected data (cf. above), our analyses required conservative assumptions because of unmarked ani- mals. In turn, we accounted for the effects of each group,

regarding grouping patterns and aggression, and each foraging individual, regarding vigilance. To this end, nested random effects within sites were allowed in each model, depending on the indicator (see *Random effects*; Supporting Information). Multicollinearity amongst covariates was tested for each full model by calculating the variance inflation factor (VIF) for all the predictors, through the R package *car* (Fox & Weisberg, 2011). All VIF values were less than two, indicating no multicol- linearity (Zuur *et al*., 2009).

For each response variable, the coefficient of predic- tors, 95% confidence intervals and variance of ran- dom effects were estimated for the top-ranked model. The significance of predictors was assessed by check- ing whether 95% confidence intervals included zero. Validation of the best models was made by visual inspection of residual patterns (Zuur *et al*., 2009). Model selection, GLMs and GLMMs were performed through the R packages *MuMIn* (Bartoń, 2012), *stats* (R Core Team, 2013), *VGAM* (Yee, 2015) and *glm- mADMB* (Bolker *et al.*, 2012).

RESULTS

Grouping patterns

Groups included a greater number of chamois in area R, where the mean group size was more than twice greater than in the other areas (Table 1a; Fig. 2A). The proportion of immature individuals (i.e. kids, yearlings and subadults) was ~40% greater in area R compared with the other sites (Table 1b; Fig. 2B). Grouping phe- nology was also influenced by the year and time of day (Table 1a,1b).

Intraspecific Aggression

The aggression rate between females was the lowest in area R (Table 1c). On average, in area R this index was lower by ~25% and ~40% compared with areas P1 and P2, respectively (Fig. 2C). The aggression rate between females was also influenced by the number of females in the group, the date and the time of day (Table 1c). We found an effect of site on aggression intensity, i.e. the probability to perform a threat (Table 1d); in areas P1 and P2, the occurrence of direct forms of aggression was more frequent, although weakly, than in area R (Table 1d). This indicator was also influenced by the date, time of day, year, age class of the opponents and type of interaction (Table 1d).

Vigilance Behaviour

For all behavioural indicators of vigilance, the effect of site was included in selected models, except for head lift rate (Supporting Information, Table S3). Although the time spent in vigilance did not vary among sites (Table 2d), the probability of occurrence of costly head lifts and the mean duration of head lifts were the low- est in area R (Fig. 3A, 3B; Table 2b,2c). Overall, behav- ioural indices of alertness were also influenced by date, year, time of day, age class, distance to the nearest cliff and percentage of costly head lifts, depending on the index (Table 2). The effect of group size on vigilance, when present, was conflicting. Head lift rate decreased with increasing group size (Table 2a). Conversely, head lift cost and duration showed a positive relationship with group size (Table 2c,2d).

Hormone levels

Levels of faecal androgen metabolites were higher in areas P1 + P2 than in area R (Fig. 4A; Table 3a). Likewise, levels of faecal cortisol metabolites were also higher in areas P1 + P2 than in area R (Fig. 4B; Table 3b). Faecal hormone metabolite levels were also influenced by age class, date and time of the day (Table 3).

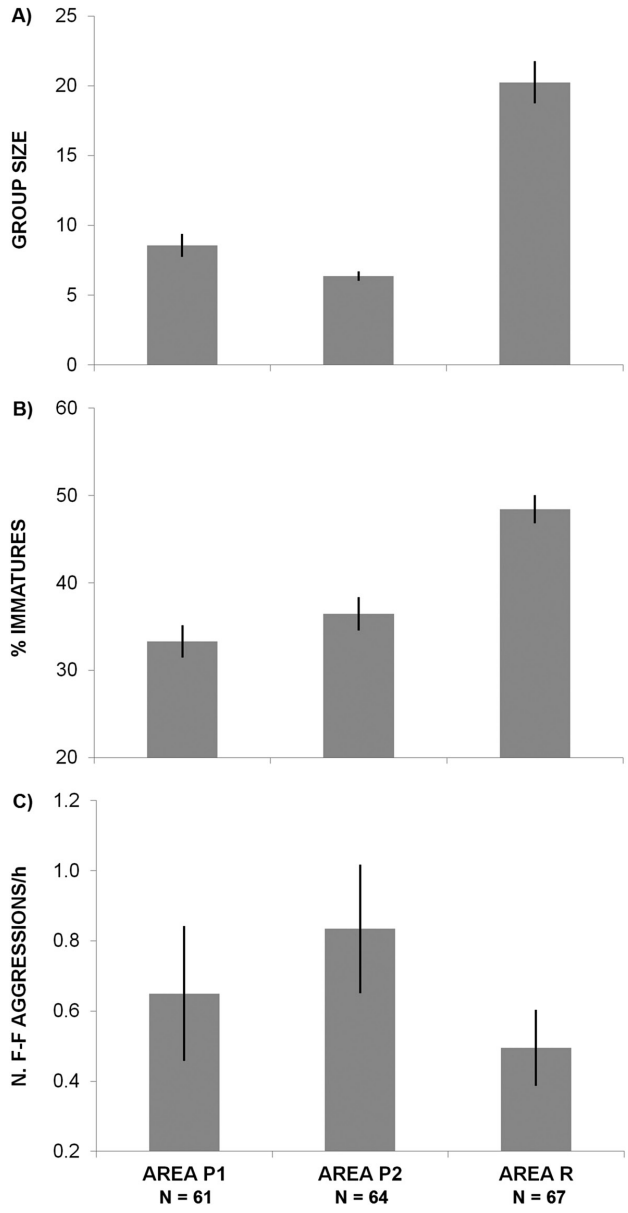


Figure 2. A–C, mean group size (A), percentage of imma- ture animals (B) and rate of female–female aggression (nor- malized by the number of females in the group; C), at each site. Error bars, SE; *N*, number of focal group bouts.

Table 1. Parameters estimated from the top-ranked models on grouping and aggressive behaviour

Indicator	Predictor	*B*	SE	95% CI
(a) Group size	Intercept	1.8154	0.3266	1.1752; 2.4556*
(focal group) variance = 0.3802	**Site (area P1)**	**0.2299**	**0.1135**	**0.0074; 0.4523***
(sampling interval) variance = 0.0010	**Site (area R)**	**1.1279**	**0.1073**	**0.9177; 1.3381***
	Date	0.0014	0.0012	−0.0010; 0.0038
	Time	−0.0587	0.0188	−0.0956; −0.0218*
	$Time^2$	0.0030	0.0008	0.0014; 0.0045*
	Year (2015)	−0.3376	0.0904	−0.5149; −0.1604*
(b) Immature animals in group	Intercept	−0.7994	0.2047	−1.2006; −0.3983*

(focal group) variance = 1.7260	**Site (area P1)**	**−0.1123**	**0.2395**	**−0.5818; 0.3571**
(sampling interval) variance = 0.0228	**Site (area R)**	**0.9581**	**0.2274**	**0.5125; 1.4038***
	Time^2	−0.0016	0.0005	−0.0026; −0.0005*
	Year (2015)	−0.3317	0.1917	−0.7074; 0.0440
(c) Aggression rate	Intercept	−1.0628	0.4887	−2.0206; −0.1049*
(focal group) variance = 0.6276	**Site (area P1)**	**−0.1576**	**0.1761**	**−0.5028; 0.1875**
(sampling interval) variance = 0.0008	**Site (area R)**	**−0.4173**	**0.1818**	**−0.7736; −0.0611***
	Date	−0.0050	0.0020	−0.0088; −0.0011*
	Time^2	0.0016	0.0008	0.0001; 0.0032*
	Number of females in group	0.0912	0.0085	0.0745; 0.1079*
(d) Aggression intensity	Intercept	−18.3874	6.3085	−30.6890; −6.0858*
(focal group) variance = 109.8000	**Site (area P1)**	**3.0403**	**1.2832**	**0.5381; 5.5425***
	Site (area R)	**−1.7294**	**1.2576**	**−4.1817; 0.7229**
	Date	0.0219	0.0283	−0.0333; 0.0771
	Time	4.5876	0.9061	2.8207; 6.3545*
	Time^2	−0.2039	0.0382	−0.2784; −0.1294*
	Aggression type (sequence)	−11.8629	2.2038	−16.1603; −7.5655*
	Sender age class (4–5 years)	7.5718	1.6294	4.3945; 10.7491*
	Sender age class (6–8 years)	5.9469	1.3551	3.3045; 8.5893*
	Sender age class (⍰ 9 years)	9.3455	1.7029	6.0249; 12.6661*

Variance of random factors is also shown. The reference categories of categorical predictors are as follows: area P2 (for site); 2014 (for year); single aggression (for aggression type), 2–3 years (for age class); and younger (for relative age of the recipient). Effect of site is shown in bold. Abbreviations: *B*, coefficient; SE, standard error; 95% CI, 95% confidence interval. Asterisks indicate the confidence intervals that do not include zero.

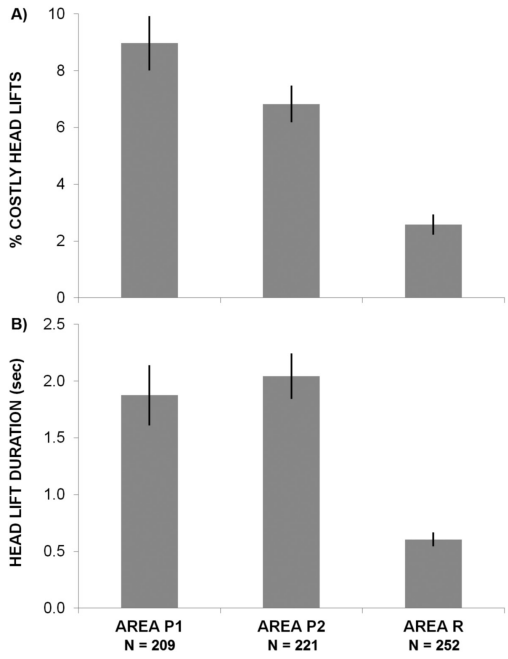
Table 2. Parameters estimated from the top-ranked models on vigilance behaviour; for generalized linear mixed models, variance of random factors is also shown

Indicator	Predictor	*B*	SE	95% CI
(a) Vigilance rate	Intercept	0.3302	0.2650	−0.1892; 0.8496
(focal individual) variance = 0.4164	Date	−0.0050	0.0010	−0.0069; −0.0031*
(sampling interval) variance < 0.0001	Time^2	0.0011	0.0004	0.0003; 0.0019*
	Year (2015)	−0.6668	0.0635	−0.7912; −0.5424
	Age class (4–5 years)	0.2882	0.1345	0.0246; 0.5518*
	Age class (6–8 years)	0.1692	0.1240	−0.0739; 0.4123
	Age class (⍰ 9 years)	0.0884	0.1216	−0.1499; 0.3267
	Cliff distance (0–25 m)	−0.0913	0.0735	−0.2353; 0.0527
	Cliff distance (> 75 m)	0.1058	0.0848	−0.0604; 0.2720
	Group size	−0.0103	0.0022	−0.0146; −0.0060*
(b) Vigilance cost	Intercept	0.0578	0.1980	−0.3302; 0.4458
(focal individual) variance = 0.0775	**Site (area P1)**	**0.0919**	**0.0350**	**0.0232; 0.1606***
	Site (area R)	**−0.1130**	**0.0426**	**−0.1964; −0.0295***
	Date	−0.0010	0.0004	−0.0018; −0.0001*
	Time	0.0667	0.0364	−0.0046; 0.1380
	Time^2	−0.0030	0.0015	−0.0060; 0.00002
	Year (2015)	0.2883	0.0290	0.2314; 0.3453*
	Group size	0.0034	0.0012	0.0010; 0.0057*
(c) Vigilance duration	Intercept	2.4827	0.2075	2.0761; 2.8893*

	Site (area P1)	**−0.1614**	**0.0752**	**−0.3088; −0.0139***
	Site (area R)	**−0.2440**	**0.0855**	**−0.4116; −0.0764***
	Date	−0.0024	0.0009	−0.0041; −0.0007*
	Group size	0.0072	0.0025	0.0022; 0.0122*
	Percentage of costly head lifts	0.0078	0.0008	0.0062; 0.0093*
(d) Vigilance effort	Intercept	2.1744	0.5590	1.0788; 3.2700*
	Site (area P1)	**0.1001**	**0.0894**	**−0.0752; 0.2754**
	Site (area R)	**−0.1433**	**0.0926**	**−0.3247; 0.0382**
	Date	−0.0112	0.0012	−0.0135; −0.0089*
	Time	−0.4214	0.1047	−0.6266; −0.2162*
	Time^2	0.0190	0.0044	0.0103; 0.0277*
	Year (2015)	−0.6887	0.0759	−0.8374; −0.5399*
	Age class (4–5 years)	0.3174	0.1506	0.0221; 0.6126*
	Age class (6–8 years)	0.1393	0.1370	−0.1292; 0.4077
	Age class (≥ 9 years)	−0.0219	0.1350	−0.2866; 0.2427
	Cliff distance (0–25 m)	−0.1066	0.0862	−0.2756; 0.0623
	Cliff distance (> 75 m)	0.1246	0.0973	−0.0662; 0.3154

The reference categories of categorical predictors are as follows: area P2 (for site); 2014 (for year); 2–3 years (for age class); and 25–75 m (for cliff distance). Effect of site, when present, is shown in bold. Abbreviations: *B*, coefficient; SE, standard error; 95% CI, 95% confidence interval. Asterisks indicate the confidence intervals that do not include zero.

Figure 3. A, B, mean percentage of costly head lifts (A) and mean duration of head lifts (B), both normalized by group size, at each site. Error bars, SE; *N*, number of focal animal bouts in which chewing/non-chewing activity was recorded.



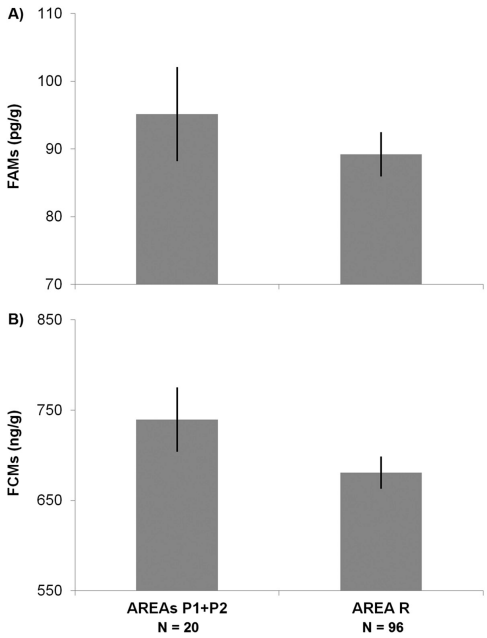


Figure 4. A, B, mean concentration of faecal androgen metabolites (FAMs; A) and faecal cortisol metabolites (FCMs; B), at each site. Error bars, SE; *N*, number of faecal samples.

Table 3. Parameters estimated from the top-ranked models on hormone levels

Indicator	Predictor	*B*	SE	95% CI
(a) Testosterone (pg g^{-1})	Intercept	53.2105	3.1390	47.3808; 59.3961*
	Site (area R)	**−5.2497**	**2.5279**	**−10.4578; −0.5150***
	Time^2	0.0228	0.0128	−0.0017; 0.0477
	Age class (subadult)	3.9488	1.9100	0.2096; 7.7534*
	Age class (adult)	53.2376	2.0621	49.2167; 57.3019*
(b) Cortisol (ng g^{-1})	Intercept	989.8371	158.1120	679.9432; 1299.7310*
	Site (area R)	**−60.0487**	**25.8718**	**−110.7564; −9.3409***
	Date	−0.7984	0.3366	−1.4581; −0.1386*
	Time	−40.9135	27.3910	−94.5988; 12.7719
	Time^2	1.9612	1.1926	−0.3763; 4.2986
	Age class (subadult)	−94.8883	35.3386	−164.1508; −25.6259*
	Age class (adult)	227.2857	27.4482	173.4882; 281.0831*

The reference categories of categorical predictors are as follows: area P1 + P2 (for site); and yearling (for age class). Effect of site is shown in bold. Abbreviations: *B*, coefficient; SE, standard error; 95% CI, 95% confidence interval. Asterisks indicate the confidence intervals that do not include zero.

DISCUSSION

For herbivores living in seasonal environments, the availability of high-quality resources in the warm months plays a key role in influencing food intake, body growth, weaning and survival of offspring, in turn affecting population dynamics (Gaillard *et al.*, 2000; Côté & Festa-Bianchet, 2001; Pettorelli *et al.*, 2007; Therrien *et al.*, 2007; Ferretti *et al.*, 2015). Our results suggest that depletion of forage can addition- ally

influence the intraspecific social behaviour of individuals, by increasing aggression and vigilance, and their endocrine correlates, in turn agreeing with competition theory (hypothesis 1).

The smallest chamois groups were observed in poor areas (i.e. areas P1 and P2), where large groups were frequently observed in past decades, when pasture was rich (i.e. up to 60 or 30 individuals, respectively; S.L., personal observations). In these sites, pasture depletion has ultimately led to a sharp decrease of chamois numbers, in the last decade, through its effects on foraging behaviour, maternal care and sur- vival of kids (Lovari *et al.*, 2014; Ferretti *et al.*, 2015; Scornavacca *et al.*, 2016). The group size of cham- ois may increase with population density (Pépin & Gerard, 2008). If so, high mortality of kids and popu- lation decrease (Ferretti *et al.*, 2015) could have led to a reduction of both group size and the proportion of younger individuals in the groups. The group size of chamois is expected to increase with the nutritional quality of pasture (Ferrari *et al.*, 1988; Bruno & Lovari, 1989); in turn, depleted food patches should support smaller groups (cf. Chirichella *et al.*, 2015, in north- ern chamois). Furthermore, individuals may tend to avoid feeding interference by aggregating in smaller groups (cf. Molvar & Bowyer, 1994). In all these cases, resource availability should be regarded as the ultim- ate determinant of the observed patterns of grouping behaviour (our prediction 1a).

Group-living herbivores coexist by balancing the costs and benefits of gregariousness, e.g. through a trade-off between food intake, vigilance and recip- rocal aggressiveness (e.g. Molvar & Bowyer, 1994). Staying in larger groups allows individuals to benefit from group vigilance as antipredatory behaviour, i.e. reduced probability of being the victim of a predatory attack, without decreasing their feeding efficiency (e.g. Pulliam, 1973; Berger, 1978). Nevertheless, feeding interference can be greater in larger groups (Molvar & Bowyer, 1994; Sirot, 2000). Accordingly, our results showed that the rate of aggression between female chamois increased as the number of females in a group increased, suggesting that individuals may trade-off higher safety against greater intraspecific competi- tion. One could have expected that the aggression rate between chamois might be higher in area R, because group size was the largest in that site, in turn deter- mining a greater probability of interaction with other individuals. Conversely, the frequency and the inten- sity (i.e. the ratio of threats to displays) of aggression between female chamois were greater in areas with the lowest pasture quality than in the rich one. These results confirm our prediction (1b) that a decrease in available food resources might lead to an increase in the level of aggressiveness between individuals; thus, interference competition enhanced aggres- sion, where resources were scarce. Our results are in agreement with the model proposed by Sirot (2000), which predicted that aggression would rise when food resources are limited, as an evolutionary stable strategy.

Several indicators of vigilance were higher in the poor areas than in the rich one, providing support to our prediction (1c). In gregarious animals, foraging individuals are expected to increase their scanning rate according to decreasing group size and higher predation risk (Lima, 1987; Roberts, 1996; Lima *et al.*, 1999; Barbosa, 2002). Local large predators (grey wolf, brown bear and golden eagle) visit all our study areas (our observations; Maiorano *et al.*, 2015; Artese *et al.*, 2017; Mancinelli *et al.*, 2018). Nevertheless, predation on chamois is negligible (cf. Material and Methods), most probably because of the steep and rugged habi- tat used by these ungulates and their antipredatory behaviour (Scornavacca & Brunetti, 2015; Baruzzi *et al.*, 2017; Šprem *et al.*, 2015), suggesting a low pre- dation risk, in all sites. Ferretti *et al.* (2015) showed that the bite rate, i.e. a clue for chamois foraging effi- ciency, was the lowest in areas P1 and P2 because of pasture depletion (but see Puorger *et al.*, 2018, for northern chamois). Feeding efficiency should be traded off by vigilance (Caraco, 1979; Ruckstuhl *et al.*, 2003; Fortin *et al.*, 2004b). If so, in poor areas, chamois would be expected to reduce their scanning behaviour to allocate more time in feeding activities (Beauchamp & Ruxton, 2003; Ruckstuhl *et al.*, 2003). Although the head lift rate and time spent in vigilance by female chamois did not differ across sites, the cost of vigi- lance, i.e. the interruption of chewing while scanning and the mean duration of head lifts, were greater in poor areas and tended to increase with group size. The mean head lift duration of individuals also increased with the proportion of costly head lifts. Costly, i.e. 'induced' vigilance, is usually performed by individu- als reacting to an outer stimulus (e.g. Blanchard & Fritz, 2007) which, in group-living species, can be rep- resented by the proximity of a potential competitor (see also McDougall & Ruckstuhl, 2018). These results strongly suggest that females grazing in areas P1 and P2 were disturbed more often than those in area R and that the higher level of inter-individual aggres- sion resulted in elevated vigilance efforts by individu- als (Treves, 2000; Favreau *et al.*, 2010; but see Slotow & Coumi, 2000; Blumstein

et al., 2002). If so, females feeding in poor areas stared at the closer grazing con- specifics for a longer time and interrupted their chew- ing activity more frequently than those feeding in the rich area, presumably to detect a potential aggres- sion earlier. In turn, their foraging efficiency would be further reduced by social monitoring, contribut- ing to limit their food intake rate in areas with poor resources (Ferretti *et al.*, 2015).
The results on grouping, aggressive and vigilance behaviour are consistent with those from the relevant endocrine correlates, supporting our prediction (1d). In most vertebrates, androgen levels are intimately linked to aggression in a mutual escalation (Adkins- Regan, 1981). Accordingly, individuals of areas P1 and P2, i.e. those where social aggression was most fre- quent, showed a greater concentration of faecal andro- gen metabolites than those inhabiting area R.

Faecal cortisol metabolites were also higher in the poor areas than in the rich one, suggesting that the endogenous stress response of chamois was greater in the former than in the latter. In turn, we suggest that pasture depletion can lead to a direct/indirect increase of hormone metabolites. A direct effect could depend on the stressful effect of lack of adequate food resources *per se*. An indirect effect might result from the stress induced by the comparatively greater risk of aggression between individuals. Moreover, the lower cortisol levels shown by chamois in the rich area, which had the largest groups, suggests that group size itself might mitigate stress (Michelena *et al.*, 2012), as the presence of conspecifics does in gregari- ous species (for a review, see Kikusui *et al.*, 2006). In all cases, levels of faecal cortisol metabolites would be driven ultimately by the availability of food resources which, in turn, would influence agonistic and grouping phenology, in addition to secretion of glucocorticoids. If this is the case, our results support the hypothesis that reduced food availability elicits stress (Kitaysky *et al.*, 1999; Clinchy *et al.*, 2004; but see Taillon & Côté, 2008; Forristal *et al.*, 2012; Le Saout *et al.*, 2016). Even while accounting for confounding predictors, our mod- els assessed statistical differences on hormonal levels across sites. Nevertheless, our results should be inter- preted cautiously because of the limited sample size in areas P1 and P2, as a result of the local low density of chamois.

Resource depletion has cascading effects on social behaviour and the endocrine responses of individu- als. The complex interplay amongst group size, feed- ing interference and vigilance behaviour has been widely discussed (Elgar, 1989; Lima, 1995; Roberts, 1996; Lima *et al.*, 1999; Beauchamp, 2001, 2008), but few studies have related it to resource availability (Beauchamp, 2009; Favreau *et al.*, 2018). In spite of the limitations resulting from our individually unmarked experimental animals (see statistical assumptions, in the Material and Methods section), our results have shown that, irrespective of group size, a lower abundance of food resources can increase aggression between conspecifics which, in turn, elicits greater levels of alertness and physiological stress. Hence, we suggest that the trade-offs between grouping behav- iour, feeding interference and vigilance might be explained ultimately by availability of resources.
Increasing temperatures determined by climatic changes are influencing vegetation worldwide, with detrimental effects on the snowbed vegeta- tion of mountainous ecosystems (Schöb *et al.*, 2009; Gottfried *et al.*, 2012; Pauli *et al.*, 2012). Cold-adapted vegetation includes forb-dominated patches, i.e. the best food resource for Apennine chamois (Ferrari *et al.*, 1988). Over the last three decades, the abun- dance of the plants most grazed by chamois has greatly decreased in our area P1, i.e. the only area where data on the composition of the vegetation were available for both the 1980s and early 2010s (Ferrari *et al.*, 1988; Lovari *et al.*, 2014). In turn, an effect of increasing ambient temperature on the reduction in the nutritional quality of pasture for chamois may be suggested (cf. Ferretti *et al.*, 2018). Moreover, in poor areas, the exploitation of resources by increasing pop- ulations of red deer has strongly accelerated pasture depletion (Lovari *et al.*, 2014; Ferretti *et al.*, 2015; cf. Anderwald *et al.*, 2016, for northern chamois). Our findings suggest that environmental changes lead- ing to pasture depletion can ultimately disrupt the social behaviour and physiology of group-living her- bivores. Behavioural plasticity is adaptive, especially when individuals cope with stressful situations and limiting factors (fish: Dill, 1983; reptiles: Cooper & Pérez-Mellado, 2012; amphibians: Relyea, 2001; birds: Gross *et al.*, 2010; mammals: Darmon *et al.*, 2014). Accordingly, our data support the theoretical model proposed by Sirot (2000), which suggests that increased aggression is an evolutionary stable strat- egy when food resources are scarce.

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S.L. and F.F. planned this study. N.F. participated in study planning, conducted most of the data collection and data analyses, wrote the first draft and participated in writing all drafts. F.F. participated in data collection and analyses and in writing up all drafts. S.L. supervised all stages of the study and participated in writing of all drafts. C.B. participated in data collection and analyses.
C.B. and N.P. participated in data collection. E.M. con- ducted hormone assays and wrote the relevant text. M.C.P. provided statistical advice and participated in data analyses. The authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Possible influencing predictors of behavioural and endocrine aspects evaluated in our analyses, with supporting references.

Table S2. Behavioural and hormonal indicators investigated through model selection, with relevant error distributions (in parentheses: link function), fixed and random (in parenthesis) effects considered in global models and number of models run. *N*, number of observations; ZT, zero truncated.

Table S3. Result of model selection: best models and models with ΔAICc < 2, each with *K*, ΔAICc, log-likelihood, AICc value and weight. The effect of site, when present, is shown in bold.